

**HOPF BIFURCATIONS IN COMPETITIVE
THREE-DIMENSIONAL LOTKA-VOLTERRA SYSTEMS**

By

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HOPF BIFURCATIONS IN COMPETITIVE THREE-DIMENSIONAL LOTKA-VOLTERRA SYSTEMS*

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Abstract. We study the space of Lotka-Volterra systems modelling three mutually competing species, each of which, in isolation, would exhibit logistic growth. By a theorem of M. W. Hirsch, the compact limit sets of these systems are either fixed points or periodic orbits. We use a geometric analysis of the surfaces $\dot{x}_i = 0$ of a system to define a combinatorial equivalence relation on the space, in terms of simple inequalities on the parameters. We list the 33 stable equivalence classes, and show that in 25 of these classes all the compact limit sets are fixed points, so we can fully describe the dynamics. We study the remaining 8 equivalence classes by finding simple algebraic criteria on the parameters, with which we are able to predict the occurrence of Hopf bifurcations and, consequently, periodic orbits.

1. Introduction.

1.1 Introduction. The growth rate of a population is generally viewed as being in some sense 'proportional' to the size of the population; where the proportionality factor, known as the *per capita* growth rate, may depend on the population size. Such growth is modelled by the ordinary differential equation

$$\dot{x} = xN(x), \quad \dot{x} \text{ denotes } \frac{dx}{dt},$$

where $x \geq 0$ is the population size at time t .

For example, when the *per capita* growth rate is $N(x) = r(1 - \frac{x}{K})$, $r, K > 0$, then there is a unique stable equilibrium at population size K . This is the familiar *logistic* growth, modelling a healthy population subject to limited resources. The healthy growth of small populations and the competition for the resources in large populations balance at the *carrying capacity* K .

A community of n interacting species is modelled similarly. The growth rate of the i th species is still considered "proportional" to its population size x_i , whilst the interaction of the species is reflected by the *per capita* growth rate, which may depend on the population sizes of any of the n species. Thus we have the system of ordinary differential equations

$$(1) \quad \dot{x}_i = F_i(x) = x_i N_i(x), \quad i = 1, \dots, n$$

where the vector $x = (x_1, \dots, x_n)$ lies in the closed positive cone \mathbb{R}_+^n .

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For distinct i and j , $\text{sign}(\frac{\partial N_i}{\partial x_j})$ and $\text{sign}(\frac{\partial N_j}{\partial x_i})$ reflect the relationship between the i th and j th species. If both quantities are positive, then the growth of each species promotes the growth of the other. That is: they cooperate. If both quantities are negative, the species compete. Finally, if the quantities are of opposite signs, then the two species have a predator-prey relationship. The matrix $DN = (\frac{\partial N_i}{\partial x_j})$ is known as the *community matrix* of the system.

When the *per capita* growth rates N_i are affine, equations 1 form the classical Lotka-Volterra system

$$\dot{x}_i = F_i(x) = x_i(b_i - (Ax)_i), \quad i = 1 \dots, n$$

which was independently introduced by Lotka and Volterra in the 1920's. Here, A is an $n \times n$ matrix.

The two-dimensional Lotka-Volterra systems are well understood: If the two species cooperate or compete there are no periodic orbits, and all bounded trajectories of the flow converge to a fixed point. The same results hold when the species have a predator-prey relationship, except for certain degenerate cases when there is a simply connected open set in $\text{Int}\mathbb{R}_+^2$ foliated by concentric periodic orbits surrounding a fixed point. These results are discussed in most elementary texts on ecology. For example, see Lotka [25] (originally published as [24]), Freedman [6], Hofbauer and Sigmund [19], May [29], [28] or Pielou [32]. For a complete dynamical classification of the two-dimensional Lotka-Volterra systems (via the topologically equivalent three-dimensional replicator systems), see E.C. Zeeman [35].

Very little is known about the dynamics of the n -dimensional Lotka-Volterra systems for $n > 2$. In 3 dimensions, isolated examples have been found of systems with periodic orbits (Coste *et al* [4], Gilpin [7]) and others with non-periodic oscillations (May and Leonard [27], Schuster *et al* [34], Phillipson *et al* [31]); but there is no classification theory with which to predict the long term behaviour of a given system.

In this paper, we work some way towards a classification theory for the Lotka-Volterra systems modelling three mutually competing species, each of which, in isolation, would exhibit logistic growth. These are the three-dimensional systems for which the parameters a_{ij}, b_i are strictly positive, and we denote by $CLV(3)$ the class of vector fields on \mathbb{R}_+^3 defining these systems. Ideally, the classification would give algebraic criteria in terms of the parameters A and b for two such systems to have topologically equivalent flows, and it would describe the dynamics in terms of algebraic invariants.

1.2 Notation. The following notation will be used repeatedly. Throughout the paper, we use italics when defining terms in the text.

$x = (x_1, \dots, x_n)$ denotes a vector in \mathbb{R}^n . The closed positive cone in \mathbb{R}^n is $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i \geq 0, \text{ each } i\}$, and the open positive cone is $\text{Int}\mathbb{R}_+^n = \{x \in \mathbb{R}_+^n : x_i \neq 0, \text{ each } i\}$. A vector x is called *positive* if $x \in \mathbb{R}_+^n$, and *strictly positive* if $x \in \text{Int}\mathbb{R}_+^n$. Similarly x is *negative* if $-x$ is positive, and *strictly negative* if $-x$ is strictly positive.

$\mathcal{X}(M)$ denotes the space of continuously differentiable vector fields on a manifold M . As a generalisation of $CLV(3)$, defined in the introduction, we denote the space of n -dimensional competitive Lotka-Volterra systems by

$$CLV(n) = \{F \in \mathcal{X}(\mathbb{R}_+^n) : F_i(x) = x_i \left(b_i - \sum_{j=1}^n a_{ij}x_j \right), a_{ij}, b_i > 0, i, j = 1, \dots, n\}$$

$F \in CLV(n)$ is clearly analytic, and we occasionally take advantage of this by ambiguously using *smooth* to mean “as smooth as necessary”.

A differentiable vector field $F \in \mathcal{X}(M)$ defines a system $\dot{x} = F(x)$ whose solution is the *local flow of F* , $\phi : M \times \mathbb{R} \rightarrow M$. The solution with initial value y is denoted by $\phi_t(y)$, and called the *orbit* or *trajectory* of y . $\alpha(y)$ and $\omega(y)$ denote the alpha and omega limit sets of y respectively.

$F, G \in \mathcal{X}(M)$ are *topologically equivalent* if there is a homeomorphism of M throwing the orbits of the flow of F onto those of the flow of G , in an orientation preserving way. This defines an equivalence relation on $\mathcal{X}(M)$, and F is *structurally stable* if it has an open neighbourhood in $\mathcal{X}(M)$ of topological equivalents. Rather than ask about the structural stability of vector fields in $CLV(n)$, which is a set of infinite codimension in $\mathcal{X}(\mathbb{R}_+^n)$, we look at stability *within* our small subset of systems. That is, we restrict our attention to vector fields in $CLV(n)$, calling F *topologically stable* if it has an open neighbourhood in $CLV(n)$ of topological equivalents. The equivalence classes in $CLV(n)$ are called the *topological classes*, and those that are open in $CLV(n)$ the *stable topological classes*. By a classification theory for $CLV(3)$, we mean precisely a description of the dynamic behaviour in each of the stable topological classes in $CLV(3)$.

We shall use *generic* to mean generic within the class of systems of the context.

1.3 Statement of Results. In §2, we describe and apply a theorem of M.W. Hirsch (theorem 2.1) to show that if $F \in CLV(n)$, then there is an invariant hypersurface, denoted Σ , such that every non-zero trajectory of $\dot{x} = F(x)$ is asymptotic (as $t \rightarrow +\infty$) to one in Σ . We call this hypersurface the *carrying simplex*, thinking of it as the balance between the growth of small populations and the competition of large populations, in analogy with the carrying capacity of the logistic model. The dynamic significance of the two-dimensional carrying simplex for $F \in CLV(3)$ is that, generically, the omega limit sets (representing the long term behaviour of the system) in $Int\mathbb{R}_+^3$ must be fixed points or periodic orbits.

§2 also contains some background material on the Hopf Bifurcation.

The aim of §§3 and 4 is to extract dynamic information from the way in which the algebraic simplicity of a Lotka-Volterra system is geometrically captured by its nullclines (the surfaces $\dot{x}_i = 0$, which are composed of affine spaces). In §3, we use a geometric analysis of these nullclines to define a combinatorial equivalence relation on $CLV(3)$, in terms of simple algebraic inequalities on the parameters. We call the equivalence classes

under this relation the *nullcline* classes, to distinguish them from the topological classes that we are really interested in. We list the 33 stable nullcline classes, and show that in 25 of these classes there are no periodic orbits, so we can fully describe their dynamics.

The remaining 8 stable nullcline classes are refined by the topological classes according to periodic orbits. In §4 we subdivide the stable nullcline classes into three-parameter families of systems corresponding to fixed nullclines, and use a yet finer geometric analysis of those nullclines to predict whether a family admits Hopf bifurcations. One consequence of these prediction results is that we have a simple means of exhibiting systems with an attracting fixed point representing an eventually stable coexistence of all three species, and others with an attracting periodic orbit, representing eventual coexistence of an oscillatory nature.

2. Background Material.

2.1 The Carrying Simplex. Our analysis of $CLV(3)$ has its foundations in the theory of competitive and cooperative dynamical systems, developed in a series of papers by M.W. Hirsch [12] – [18]. In particular, we shall apply the main theorem of part III of this series, discussed below, to show that for $F \in CLV(n)$, the omega limit sets of the system $\dot{x} = F(x)$ are precisely those of a uniquely determined $(n - 1)$ -dimensional invariant hypersurface. For $n = 2$, this implies that the omega limit sets must be fixed points; whilst for $n = 3$, we have an invariant two-dimensional surface, on which (by Poincaré-Bendixson theory, see [30], [11]) every limit set is either a fixed point, periodic orbit, or a chain of fixed points $\{p_i\}$, “joined” by regular orbits $\{\gamma_j\}$. (I.e. $\alpha(\gamma_j), \omega(\gamma_j) \in \{p_i\}$, for each j).

A system $\dot{x} = F(x)$ of differential equations on \mathbb{R}^n is called *competitive* if $\frac{\partial F_i}{\partial x_j} \leq 0$, for $j \neq i$, and *cooperative* if $\frac{\partial F_i}{\partial x_j} \geq 0$, for $j \neq i$; where F_i, x_i are the i th components of F and x respectively. These names are clearly suggestive. Since each $x_i > 0$, the competition and cooperation conditions are precisely those described in the introduction as reflecting the type of interaction between species. There is a famous comparison principle of Kamke [23] which states that the forward flow of a cooperative system is monotone, meaning that it preserves the partial ordering on \mathbb{R}^n . Note that under time-reversal (changing the independent variable from t to $-t$) a cooperative system becomes competitive, and vice versa, so that we have, equivalently, monotonicity of the backward flow of a competitive system.

In his series of papers [12] – [18], Hirsch exploits these order preserving properties to analyse the geometry and dynamics of compact limit sets of competitive and cooperative systems on \mathbb{R}^n , and subsequently to discuss the structural stability of these systems in three dimensions. Part III of the series, entitled *Competing Species*, deals with competitive systems of the form

$$(2) \quad \dot{x}_i = F_i(x) = x_i N_i(x) \quad i = 1, \dots, n$$

on \mathbb{R}_+^n , under the added assumptions of dissipation and irreducibility, defined below.

System 2 is *dissipative* if there is a compact invariant set which uniformly attracts each compact set of initial values. If we permit the existence of a point $\infty \in \mathbb{R}_+^n$, then dissipation can be thought of as “a repeller at ∞ ”. The system is *irreducible* if the community matrix DN is irreducible at every point in $\text{Int}\mathbb{R}_+^n$. This is a mild genericity condition, meaning that for any $p \in \text{Int}\mathbb{R}_+^n$, and distinct $i, j \in 1, \dots, n$, there is a finite sequence $i = k_1, \dots, k_m = j$ such that $\frac{\partial N_{k_r}}{\partial x_{k_{r+1}}}(p) \neq 0$ for $r = 1, \dots, m - 1$. The interpretation is that each species influences every other species, either directly or indirectly. Both of these conditions are satisfied by $F \in CLV(n)$.

In part II of the series [13], Hirsch shows that in a cooperative system satisfying the genericity condition that all fixed points are simple, almost every point (in the sense of Lebesgue measure) whose forward orbit has compact closure converges to an attracting fixed point. This can be restated, via time-reversal, to say that for a generic competitive system, almost every point whose backward orbit has compact closure lies in the basin of repulsion of a repelling fixed point. Now, if the generic competitive system is also dissipative, we can think of ∞ as being a repelling fixed point, and conclude that almost every point of \mathbb{R}_+^n lies in the basin of repulsion of a repelling fixed point.

The main result of part III of the series [15] is that for each repelling fixed point $p_i \in \text{Int}\mathbb{R}_+^n$, the boundary of the basin of repulsion of p_i contains a forward invariant subset M_i of a particularly simple topological and geometric nature; these M_i are disjoint, and every omega limit set in $\text{Int}\mathbb{R}_+^n$ is an omega limit set of the system restricted to an M_i . To be more precise about the M_i , each one is a Lipschitz submanifold, homeomorphic to \mathbb{R}^{n-1} , and everywhere transverse to all positive rays in \mathbb{R}^n (so that no two points in an M_i are ordered by the partial ordering on \mathbb{R}^n).

In the simple event that there are no finite repelling fixed points in $\text{Int}\mathbb{R}_+^n$, the family of submanifolds $\{M_i\}$ described above reduces solely to the boundary of the basin of repulsion of ∞ , whose closure we denote by Σ . This event is guaranteed when the origin (necessarily a fixed point of system 2) repels, and the community matrix DN at all other fixed points has strictly negative entries. We state the theorem in this weak version, and apply it to $F \in CLV(n)$.

THEOREM 2.1 (HIRSCH). *Let $\dot{x}_i = F_i(x) = x_i N_i(x)$, $i = 1, \dots, n$ be a competitive, dissipative system on \mathbb{R}_+^n , for which the origin repels, and such that DN has strictly negative entries at every other (finite) fixed point. Then every trajectory in $\mathbb{R}_+^n \setminus \{0\}$ is asymptotic to one in Σ , and Σ is homeomorphic to the unit simplex in \mathbb{R}_+^n by radial projection.*

Remark. So far we have only defined Σ intuitively as the boundary of the basin of repulsion of the fictitious fixed point at ∞ . This can easily be made rigorous by defining $R(\infty) = \{x \in \mathbb{R}_+^n : \alpha(x) = \infty\}$, and $\Sigma = \partial R(\infty)$. The unit simplex in \mathbb{R}_+^n is defined to be $\{x \in \mathbb{R}_+^n : \sum_{i=1}^n x_i = 1\}$.

COROLLARY 2.2. *Let $\dot{x} = F(x)$, where $F \in CLV(n)$. Then there is an invariant hypersurface Σ , homeomorphic to the unit simplex in \mathbb{R}_+^n by radial projection, such that every trajectory in $\mathbb{R}_+^n \setminus \{0\}$ is asymptotic to one in Σ .*

Remark. This means that the omega limit sets of the system are precisely those of the system restricted to the invariant hypersurface Σ , which we call the *carrying simplex*. Recall that for $x \notin \Sigma$, $\alpha(x)$ is either 0 or ∞ , so that *all* the finite limit sets in $\mathbb{R}_+^n \setminus \{0\}$ lie on Σ . For $n = 2$, the carrying simplex is a curve, and the limit sets must therefore be fixed points; whilst for $n = 3$, the carrying simplex is a two-dimensional surface, on which we can use Poincaré-Bendixson theory. In §3, we shall show that for $F \in CLV(n)$ there is generically at most one fixed point in $Int\Sigma$ (the interior of Σ), and this fixed point is simple, so that a limit set in $Int\Sigma$ is either a fixed point or a periodic orbit.

Proof of the corollary. For $F \in CLV(n)$, the system is certainly competitive. Writing

$$F_i(x) = x_i \left(b_i - \sum_{j=1}^n a_{ij}x_j \right), \quad \text{for some } a_{ij}, b_i > 0$$

we see that for $|x|$ sufficiently large, $F(x)$ is a negative vector. Thus by Kamke's comparison principle, $|\phi_{-t}(x)|$ is monotone increasing with t , $\lim_{t \rightarrow \infty} |\phi_{-t}(x)| = \infty$, and the system is dissipative. Similarly, for $|x|$ sufficiently small but non-zero, $F(x)$ is a positive vector, whilst $F(0) = 0$, so that the origin is a repelling fixed point.

In the notation of theorem 2.1, $N_i(x) = b_i - \sum_{j=1}^n a_{ij}x_j$. So $\frac{\partial N_i}{\partial x_j} = -a_{ij} < 0$, $\forall i, j$ and the community matrix has strictly negative entries everywhere, and *a fortiori* at the fixed points. Now we can apply theorem 2.1. \square

2.2 The Hopf Bifurcation. As mentioned in the previous section, for generic $F \in CLV(3)$, any limit set in $Int\mathbb{R}_+^3$ of the system $\dot{x} = F(x)$ is either a fixed point or a periodic orbit. The algebraic simplicity of Lotka-Volterra systems makes the location of fixed points easy. We approach the more subtle question of periodic orbits by considering one-parameter families of systems, and applying the Hopf Bifurcation Theorem, which describes the development of periodic orbits from a fixed point, whose stability changes at some critical value of the parameter.

This phenomenon was first described by Poincaré [33, pp. 131–33] in 1892. The two-dimensional theorem was extensively discussed by Andronov and Witt [1] in 1930, and was extended to higher dimensions by E. Hopf [20] in 1942.

We shall discuss the heuristic ideas and state the theorem, ready for later use. The proof of the theorem is technically rather complicated, and for that we refer the reader to the literature. See, for example, any of the following books: Arnold [2], Marsden and McCracken [26], Hassard, Kazarinoff and Wan [10]; or the translation (in [26]) of Hopf's original paper [20] by Howard and Kopell [21].

Given a vector field $F_0 : \mathbb{R}^n \rightarrow \mathbb{R}^n$, and the associated system $\dot{x} = F_0(x)$ on \mathbb{R}^n , the fixed points are given by the zeros of F_0 . Analysis of a generic fixed point x_0 is straightforward: The Hartman-Grobman theorem (see Hartman [8], Irwin [22] or Palis and De Melo [30]) says that in a neighbourhood of x_0 , F_0 is topologically equivalent to its linear part $DF_0(x_0)$ at x_0 . Indeed, the topological type of the fixed point is determined by the distribution of the eigenvalues of $DF_0(x_0)$ in the complex plane, where the genericity of x_0 ensures that all of these eigenvalues lie off the imaginary axis. If $DF_0(x_0)$ has n_+ eigenvalues with strictly positive real part, and n_- eigenvalues with strictly negative real part, (eigenvalues are counted with multiplicity so that $n_+ + n_- = n$) then the fixed point x_0 has an unstable manifold of dimension n_+ , and a stable manifold of dimension n_- , intersecting transversally at x_0 . Moreover, this dynamic behaviour is preserved under small perturbations of the system. Consider a smooth one-parameter family of systems $\dot{x} = F_\mu(x)$ through the original system $\dot{x} = F_0(x)$, where the parameter μ is real. By the Implicit Function Theorem, there is a curve of fixed points $x_\mu = x(\mu)$ through x_0 . The eigenvalues of $DF_\mu(x_\mu)$ depend continuously on the matrix entries, which in turn depend continuously on the parameter μ . Thus there is a neighbourhood M of 0 in \mathbb{R} , such that for $\mu \in M$, the system $\dot{x} = F_\mu(x)$ has a fixed point near x_0 of the same topological type as x_0 .

However, for values of μ far from 0, one or more of the eigenvalues of $DF_\mu(x_\mu)$ may cross the imaginary axis, so that their distribution in the complex plane changes. As this happens, and an eigenvalue approaches the imaginary axis, the radius of the neighbourhood of x_μ on which F_μ is topologically equivalent to its linear part shrinks to 0, and a metamorphosis of the phase portrait takes place. For example, as a simple real eigenvalue passes through the origin, a new pair of fixed points may bifurcate out of (or amalgamate into) our fixed point x_μ . We shall see later that within the class $CLV(n)$, the limited number of fixed points guarantees that this does not occur in $Int\mathbb{R}_+^n$, so we shall not delve into the details. The other generic possibility is that a simple complex conjugate pair of eigenvalues crosses the imaginary axis. (Recall that the non-real eigenvalues of a real matrix occur in complex conjugate pairs.) This is the condition for a Hopf Bifurcation, in which, analogously, a periodic orbit may bifurcate out of (or be amalgamated into) our fixed point.

Note that we use genericity to mean that any nearby one-parameter family of systems exhibits the same phenomenon of a curve of fixed points on which a simple complex conjugate pair of eigenvalues crosses the imaginary axis. The bifurcation is thus referred to as a codimension-one bifurcation. In the space of vector fields under investigation, we can imagine the hypersurface of systems exhibiting a fixed point with a complex conjugate pair of eigenvalues on the imaginary axis, and our generic one-parameter family joining one stable topological class to another, crossing the hypersurface transversally on its way.

For simplicity, we state an analytic version of the Hopf Bifurcation Theorem on \mathbb{R}^n . This is by no means the most general version of the theorem, but it is sufficient for our needs.

THEOREM 2.3 (HOPF BIFURCATION THEOREM). *Let $F_\mu : \mathbb{R}^n \rightarrow \mathbb{R}^n$ be an analytic one-parameter family of vector fields with a corresponding one-parameter family x_μ of isolated fixed points, so that $F_\mu(x_\mu) = 0$, where the real parameter μ ranges over a neighbourhood of 0 in \mathbb{R} . Assume that $DF_\mu(x_\mu)$ has a simple pair of complex conjugate eigenvalues $\lambda_\mu, \bar{\lambda}_\mu$ that cross the imaginary axis with strictly positive speed as μ passes through 0. Writing $\lambda_\mu = \alpha_\mu + i\omega_\mu$, these conditions translate to $\alpha_0 = 0$, $\omega_0 > 0$ and $\alpha'_0 > 0$. Assume also that the remaining $n - 2$ eigenvalues of $DF_0(x_0)$ have strictly negative real parts. Then the one-parameter family of systems $\dot{x} = F_\mu(x)$ has a one-parameter family of periodic orbits. That is, for some $\epsilon_1 > 0$ sufficiently small, there is an analytic function $\mu : (0, \epsilon_1) \rightarrow \mathbb{R}$ such that for each $\epsilon \in (0, \epsilon_1)$, there is a periodic orbit p_ϵ of the system $\dot{x} = F_{\mu(\epsilon)}(x)$. The function μ , if not identically zero, is either strictly positive or strictly negative on $(0, \epsilon_1)$. Moreover, there is a neighbourhood U of $0 \in \mathbb{R}^n$ and $\mu_1 > 0$ such that for $|\mu| < \mu_1$, any periodic orbit of F_μ in U is one of the p_ϵ described above.*

Remark. The theorem tells us that we have a single one-parameter family of periodic orbits existing in conjunction with our one-parameter family of fixed points, and that with respect to the original parameter μ , this family exists in exactly one of the cases (i) $\mu > 0$, (ii) $\mu = 0$ or (iii) $\mu < 0$. These three possibilities are illustrated in figure 1 for systems on \mathbb{R}^2 . The general n -dimensional case can be thought of similarly by restricting attention to certain two-dimensional hyperbolic and pseudo-hyperbolic manifolds of the fixed point. (To be precise: the two-dimensional weakly stable manifold whilst $\mu < 0$, a centre manifold whilst $\mu = 0$ and the unstable manifold whilst $\mu > 0$.)

In case (i), the fixed point is stable for $\mu < 0$, but at the bifurcation value $\mu = 0$, sacrifices its stability to the newly developed periodic orbit. This is known as a Supercritical Bifurcation, and is of most interest experimentally, for the simple reason of observability. Case (iii) is the Subcritical Bifurcation, in which the unstable periodic orbit and stable fixed point coexist for $\mu < 0$, amalgamating at $\mu = 0$ to result in an unstable fixed point. Case (ii) is the degenerate situation of the whole family of periodic orbits existing together at the bifurcation value $\mu = 0$, foliating a neighbourhood of the fixed point.

We should note that at its full strength, the Hopf Bifurcation Theorem states far more than this: It gives estimates for the period and radii of the periodic orbits in terms of ω_0 and $\mu(\epsilon)$ respectively, as well as determining the stability properties of these periodic orbits. In our situation, the geometric simplicity of the three-dimensional Lotka-Volterra systems renders these technicalities unnecessary.

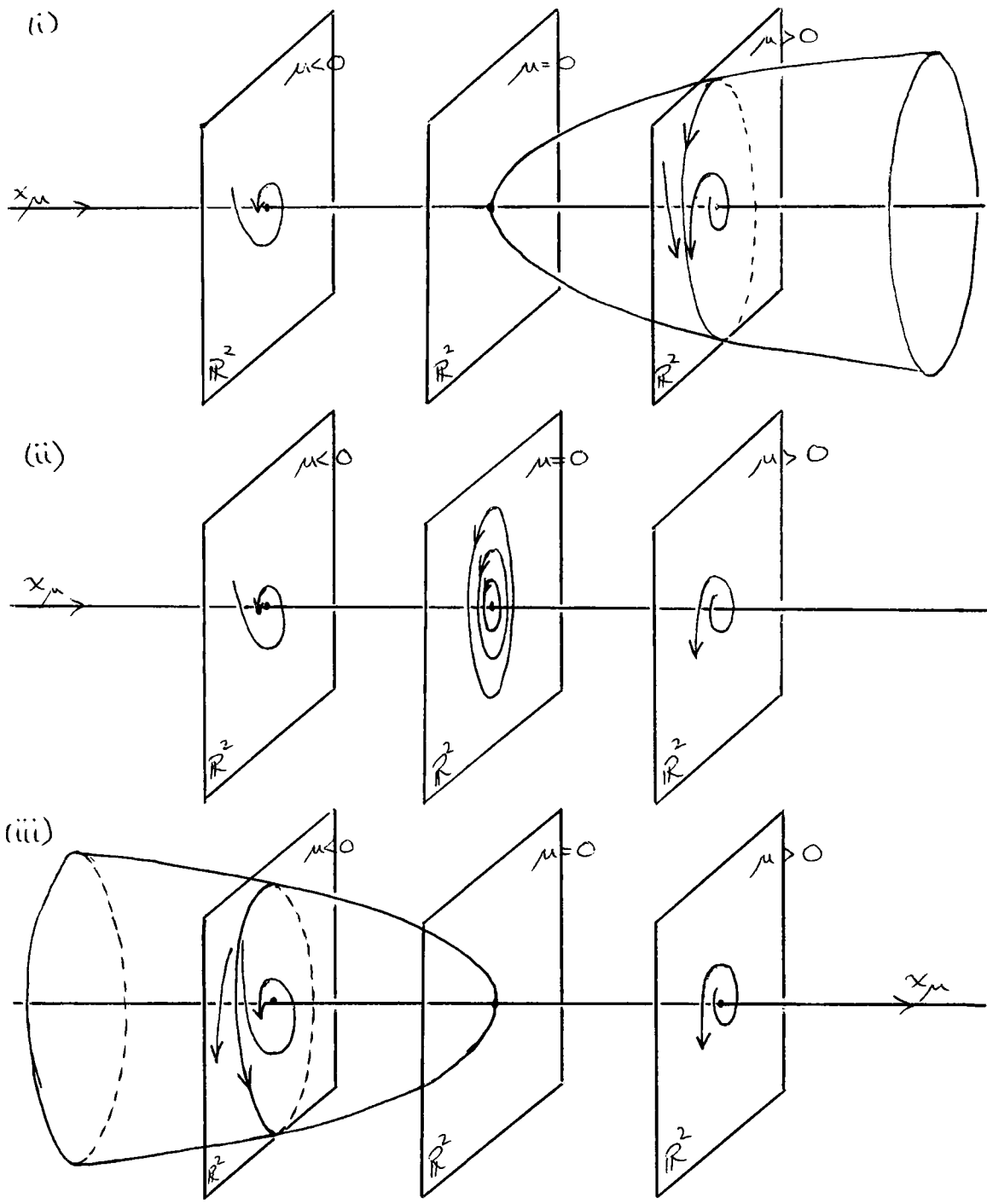


Figure 1: The Hopf bifurcation

3. Classification by Nullcline Equivalence.

3.1 The Two-Dimensional Case. To pave the way for the three-dimensional analysis, we now present the familiar results of the two-dimensional competitive Lotka-Volterra systems, described in the introduction, in a manner that generalises to higher dimensions.

We saw in §2.1 that for $F \in CLV(2)$, the non-zero finite limit sets of the system $\dot{x} = F(x)$ are all fixed points, and that they lie on an invariant curve Σ , homeomorphic to the unit simplex in \mathbb{R}_+^2 by radial projection.

The location of these fixed points is easy. They lie at the intersections of the surfaces $\dot{x}_i = 0$ of the system, which we call the *nullclines*. In what follows, we use a geometric analysis of the configuration of the nullclines to define a combinatorial equivalence relation on $CLV(2)$, called *nullcline equivalence*, whose equivalence classes reflect not only the location but also the dynamic behaviour at the fixed points. Thus we show that, in the two-dimensional case, the stable nullcline classes coincide precisely with the stable topological classes. In §4, we shall see in contrast that, when we follow the same program of investigation for $CLV(3)$, defining the analogous nullcline equivalence relation, the stable nullcline classes do *not* always coincide with the stable topological classes, but instead are refined by them according to periodic orbits.

Location of the Fixed Points.

The nullclines are given by

$$\dot{x}_i = 0 \Leftrightarrow x_i(b_i - (Ax)_i) = 0 \Leftrightarrow \begin{cases} x_i = 0 \\ \text{or } (Ax)_i = b_i \end{cases}.$$

So the i th nullcline is the union of the i th coordinate axis, and another line $N_i = \{(x_1, x_2) : a_{i1}x_1 + a_{i2}x_2 = b_i\}$, with positive normal vector (a_{i1}, a_{i2}) , and positive axial intercepts $(\frac{b_i}{a_{i1}}, 0)$ and $(0, \frac{b_i}{a_{i2}})$. Generically, there are four intersections of these nullclines in \mathbb{R}^2 , and they can be classified into three types depending on their position relative to the coordinate axes, as follows:

- (1) The origin 0.
- (2) The two *axial* fixed points $R_1 = (\frac{b_1}{a_{11}}, 0)$ and $R_2 = (0, \frac{b_2}{a_{22}})$, where the line N_i meets the x_i axis.
- (3) The *interior* fixed point $P = (p_1, p_2)$ at the intersection of the lines N_1 and N_2 . Note that $AP = b$

Recall that we are only interested in those fixed points that lie in \mathbb{R}_+^2 . This includes the origin, and each R_i , but not necessarily P .

PROPOSITION 3.1. *The configuration of the lines N_i determines the dynamic behaviour of the flow at the fixed points R_i .*

Proof. Each coordinate axis x_i is invariant, and is an eigenspace of DF_{R_i} , along which R_i attracts with associated eigenvalue $-b_i$. To fix our ideas, consider R_1 , and make the

genericity assumption that DF_{R_1} has distinct eigenvalues. It would be easy to calculate the second eigenvalue and associated eigenvector directly from the matrix DF_{R_1} ; but to generalise that method to higher dimensions would present difficult algebraic problems. Instead, we use geometric methods, and determine the qualitative behaviour at R_1 by considering the way that \mathbb{R}_+^2 is partitioned by the line N_2 , and where R_1 sits in this partition. Recall that N_2 is part of the nullcline on which $\dot{x}_2 = 0$. There are two components in $\mathbb{R}_+^2 \setminus N_2$: one bounded component, on which $\dot{x}_2 \geq 0$ and one unbounded component, on which $\dot{x}_2 \leq 0$. Thus if R_1 lies in the bounded component of $\mathbb{R}_+^2 \setminus N_2$, then $\dot{x}_2 \geq 0$ in a neighbourhood of R_1 in \mathbb{R}_+^2 , and in particular, R_1 is a saddle point, repelling along the second eigendirection. If, on the other hand, R_1 lies in the unbounded component of $\mathbb{R}_+^2 \setminus N_2$, then R_1 is an attractor, attracting along that eigendirection. In a similar fashion, we can determine the qualitative behaviour at R_2 . See figure 2. \square

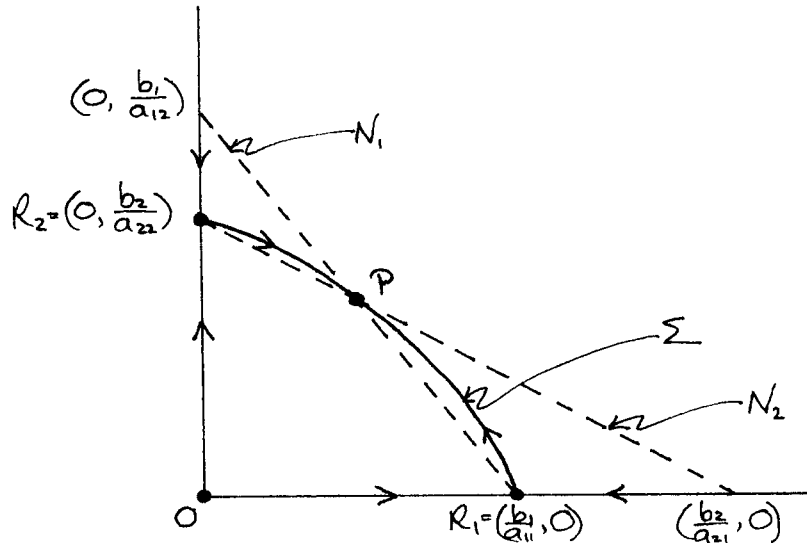


Figure 2: The behaviour at the fixed points of F .

COROLLARY 3.2. *The configuration of the lines N_i determines the dynamic behaviour of the flow in \mathbb{R}_+^2 .*

Proof. This is immediate, since the carrying simplex Σ is globally attracting for \mathbb{R}_+^2 , and the behaviour on Σ (since one-dimensional) is determined by the behaviour at the axial fixed points R_i . \square

Example. Consider the case $\frac{b_1}{a_{11}} < \frac{b_2}{a_{21}}$ and $\frac{b_1}{a_{12}} > \frac{b_2}{a_{22}}$ pictured in figure 2. Each R_i is in the bounded component of $\mathbb{R}_+^2 \setminus N_j$ ($i \neq j$), and is thus a saddle point of F . Moreover, the lines N_i necessarily cross in $Int\mathbb{R}_+^2$ so that $P \in Int\mathbb{R}_+^2$, and the carrying simplex Σ is composed of the fixed points R_i and P , joined by the unstable manifolds of the R_i . Therefore P attracts along Σ , and since Σ is globally attracting on $Int\mathbb{R}_+^2$, so is P .

The proof of proposition 3.1 has given precision to our notion of nullcline configuration. Geometrically, we characterised this configuration by the relative positions of the axial intercepts of the nullclines. This translates into an algebraic characterisation by the values of $\text{sgn}(\frac{b_i}{a_{ii}} - \frac{b_j}{a_{ji}})$, $i \neq j$.

Note that since $\frac{b_i}{a_{ii}}$ is just the i th coordinate of the axial fixed point R_i , we have

$$\text{sgn}\left(\frac{b_i}{a_{ii}} - \frac{b_j}{a_{ji}}\right) = \text{sgn}\left(a_{ji}\frac{b_i}{a_{ii}} - b_j\right) = \text{sgn}((AR_i)_j - b_j)$$

where $(AR_i)_j$ is the j th component of AR_i .

Although this seems a rather cumbersome way of writing a simple inequality, we shall see that it generalises well to higher dimensions. For that reason we adopt it here, to give a precise definition of nullcline configuration, with which we can define the nullcline equivalence relation on $CLV(2)$.

DEFINITION 3.3. Let $F \in CLV(2)$. The nullcline configuration of F is given by the values of

$$\text{sgn}((AR_i)_j - b_j), \quad \text{for } i \neq j, \quad i, j = 1, 2$$

modulo permutation of the indices.

Remark. Permitting permutation of the indices ensures that our definition is independent of the labelling of the coordinate axes.

DEFINITION 3.4. Let $F, G \in CLV(2)$. We say that F and G are nullcline equivalent if and only if they have the same nullcline configurations.

This clearly defines an equivalence relation on $CLV(2)$. We call the equivalence classes under this relation the *nullcline classes*, and, as usual, say that F is *nullcline stable* iff F has a neighbourhood of equivalents. The *stable nullcline classes* are those nullcline classes whose elements are nullcline stable.

The following proposition and its corollaries are immediate.

PROPOSITION 3.5. Let $F \in CLV(2)$. F is nullcline stable if and only if $\text{sgn}((AR_i)_j - b_j) \neq 0$, for $i \neq j$.

COROLLARY 3.6. The stable nullcline classes have open dense union in $CLV(2)$.

COROLLARY 3.7. There are 3 stable nullcline classes in $CLV(2)$.

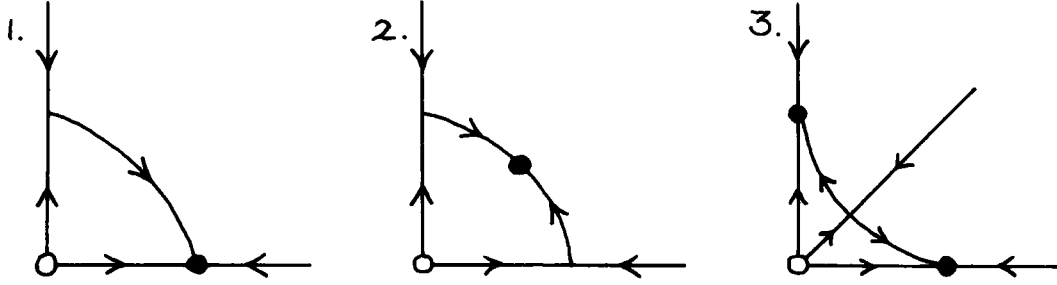


Figure 3: The two-dimensional stable nullcline classes. A fixed point is represented by a closed dot \bullet if it attracts, by an open dot \circ if it repels, and by the intersection of its hyperbolic manifolds if it is a saddle.

Corollary 3.2 enables us to describe these 3 stable nullcline classes by their dynamics. We do this in figure 3, listing a representative from each class by its phase portrait on \mathbb{R}_+^2 . A fixed point is represented by a closed dot \bullet if it attracts; by an open dot \circ if it repels, and by the intersection of its hyperbolic manifolds if it is a saddle.

Note that in the cases when the lines N_i meet at $P \in \text{Int}\mathbb{R}_+^2$, then the nullcline configuration is determined by the relative slopes of the lines N_i . But the equation for N_i is simply $(Ax)_i = b_i$, so that N_i has normal vector n_i , composed of the elements of the i th row of A . The relative sizes of the slopes of these n_i , and hence of the N_i , are determined by $\text{sgn}(\det A)$. Indeed, P is attracting when $\det A > 0$, and repelling when $\det A < 0$. This is a convenient relationship between the dynamics and the algebra, which we shall use repeatedly in §4. When $\det A = 0$ there is a linear dependence between the rows of A , so that if the lines N_i meet at all they coincide. Thus F has a whole line of fixed points, and is neither topologically nor nullcline stable.

It is clear that if $F \in \text{CLV}(2)$ is topologically stable, it is also nullcline stable. Thus the stable topological classes refine the stable nullcline classes. The following theorem shows that this refinement is in fact trivial, so that nullcline stability characterises topological stability for $\text{CLV}(2)$.

THEOREM 3.8. *In $\text{CLV}(2)$, the stable nullcline classes coincide precisely with the stable topological classes.*

Proof. We first show that every vector field $F \in \text{CLV}(2)$ has a global Liapunov function V_F on \mathbb{R}_+^2 , varying continuously with the parameters of F . We then use the method of fundamental domains together with the added structure given by the level sets of V_F to construct a topological equivalence between stable nullcline equivalent vector fields.

Let $F \in CLV(2)$ be given as usual by

$$F_i(x) = x_i \left(b_i - \sum_{j=1}^2 a_{ij} x_j \right) \quad i = 1, 2$$

and consider the quadratic function $V_F : \mathbb{R}^2 \rightarrow \mathbb{R}$ defined by

$$V_F(x) = a_{21} x_1 \left(\sum_{j=1}^2 a_{1j} x_j - 2b_1 \right) + a_{12} x_2 \left(\sum_{j=1}^2 a_{2j} x_j - 2b_2 \right)$$

When $\det A > 0$, the graph of V_F is a paraboloid with minimum at P ; and when $\det A < 0$, V_F has a saddle point at P . For $x \in \mathbb{R}_+^2$

$$\nabla V_F \cdot F(x) = -2a_{21} x_1 \left(b_1 - \sum_{j=1}^2 a_{1j} x_j \right)^2 - 2a_{12} x_2 \left(b_2 - \sum_{j=1}^2 a_{2j} x_j \right)^2 \leq 0$$

since $a_{21}, a_{12} > 0$; and $\nabla V_F \cdot F(x) = 0$ iff x is a fixed point of F . Thus V_F is a global Liapunov function for F , meaning that the value of V_F decreases with time along non-constant orbits of F , and these orbits are everywhere transverse to the level sets of V_F .

Now choose two stable nullcline equivalent vector fields $F, \tilde{F} \in CLV(2)$. To fix our ideas, assume F, \tilde{F} are in stable nullcline class 3. Then F has carrying simplex Σ with attracting fixed points R_1, R_2 and a saddle at P , whilst \tilde{F} has carrying simplex $\tilde{\Sigma}$ with attracting fixed points \tilde{R}_1, \tilde{R}_2 and a saddle at \tilde{P} . The following type of construction works equally well for nullcline classes 1 and 2.

Let V and \tilde{V} be the Liapunov functions for F and \tilde{F} respectively. That is, $V = V_F$ and $\tilde{V} = V_{\tilde{F}}$ as defined above. We shall use V and \tilde{V} to construct a homeomorphism of \mathbb{R}_+^2 throwing orbits of F onto those of \tilde{F} in an orientation preserving manner.

Since V is a Liapunov function for F , we know that

$$0 = V(0) > V(P) > V(R_1), V(R_2)$$

and similarly

$$0 = \tilde{V}(0) > \tilde{V}(\tilde{P}) > \tilde{V}(\tilde{R}_1), \tilde{V}(\tilde{R}_2)$$

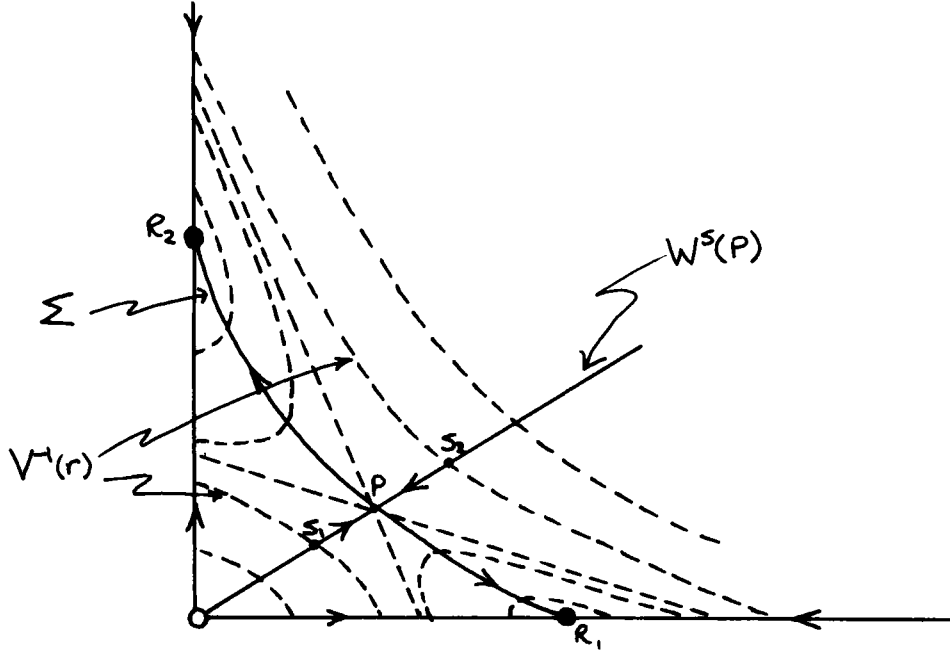


Figure 4: Construction of the homeomorphism H .

After any necessary permutation of the axes, or perturbation of V or \tilde{V} to nearby Liapunov functions, we may assume that $V(R_1) > V(R_2)$ and $\tilde{V}(\tilde{R}_1) > \tilde{V}(\tilde{R}_2)$. So we can choose a homeomorphism $h : \mathbb{R} \rightarrow \mathbb{R}$ such that

$$h(0) = 0, \quad h(V(P)) = \tilde{V}(\tilde{P}), \quad \text{and} \quad h(V(R_i)) = \tilde{V}(\tilde{R}_i), \quad i = 1, 2.$$

Now choose $r \in \mathbb{R}$ such that $V(P) < r < 0$, and consider the level set $V^{-1}(r)$ of V . The choice of r ensures that $V^{-1}(r)$ is a hyperbola, with centre at P , and is a fundamental domain for F on $\mathbb{R}_+^2 \setminus \Sigma \cup \{0\}$, meaning that it uniquely intersects every orbit of F in $\mathbb{R}_+^2 \setminus \Sigma \cup \{0\}$. In particular, let S_1, S_2 ($|S_1| < |S_2|$, say) be the two points where the stable manifold of P ($W^s(P)$) meets $V^{-1}(r)$. See figure 4.

Similarly, $\tilde{V}(\tilde{P}) < h(r) < 0$, so $\tilde{V}^{-1}(h(r))$ is a fundamental domain for \tilde{F} on $\mathbb{R}_+^2 \setminus \tilde{\Sigma} \cup \{0\}$, and meets the stable manifold of \tilde{P} at \tilde{S}_1, \tilde{S}_2 , where $|\tilde{S}_1| < |\tilde{S}_2|$, say.

Let $h_r : V^{-1}(r) \rightarrow \tilde{V}^{-1}(h(r))$ be a homeomorphism between the fundamental domains, preserving the axes, and such that $h_r(S_i) = \tilde{S}_i$, $i = 1, 2$. We can now use h and h_r to define the required homeomorphism H of \mathbb{R}_+^2 as follows: On $\mathbb{R}_+^2 \setminus \Sigma \cup \{0\}$, define

$$H(x) = \tilde{\mathcal{O}}(h_r(\mathcal{O}(x) \cap V^{-1}(r))) \cap \tilde{V}^{-1}(h(V(x)))$$

where $\mathcal{O}(x)$ and $\tilde{\mathcal{O}}(x)$ denote the orbits of x under F and \tilde{F} respectively. Then $H : \mathbb{R}_+^2 \setminus \Sigma \cup \{0\} \rightarrow \mathbb{R}_+^2 \setminus \tilde{\Sigma} \cup \{0\}$ throws orbits of F onto orbits of \tilde{F} , and level sets of V onto

level sets of \tilde{V} . By the transversality of these structures, H is everywhere continuous, and hence extends to a homeomorphism of \mathbb{R}_+^2 . \square

3.2 The Three-Dimensional Case. From the theorem of Hirsch (theorem 2.1, §2.1), we know that for $F \in CLV(3)$, every non-zero trajectory of the system $\dot{x} = F(x)$ is asymptotic to one in the carrying simplex Σ , and that Σ is homeomorphic to the unit simplex in \mathbb{R}_+^3 by radial projection.

We now pursue the program of investigation described in the previous section to define a nullcline equivalence relation on $CLV(3)$. We list the stable nullcline classes, of which there are 33, and conjecture that 25 of these are in fact stable topological classes, since all the limit sets are fixed points. We shall investigate the way in which the 8 remaining stable nullcline classes are refined by the topological classes in §4.

Location of the Fixed Points.

As before, the nullclines are given by

$$x_i = 0 \Leftrightarrow x_i(b_i - (Ax)_i) = 0 \Leftrightarrow \begin{cases} x_i = 0 \\ \text{or } (Ax)_i = b_i \end{cases}$$

So now the i th nullcline is the union of the i th coordinate plane, and another plane N_i with positive normal vector and positive axial intercepts. Any fixed point of the system lies at an intersection of all three nullclines. Generically there are 8 such intersections in \mathbb{R}^3 , and they can be classified into 4 types relative to the coordinate axes.

- (1) The origin 0.
- (2) The three *axial* fixed points R_i , where the plane N_i meets the x_i axis.
- (3) The three *planar* fixed points Q_{ij} , where the planes N_i and N_j meet on the coordinate plane $x_k = 0$. (Here i, j, k are distinct.)
- (4) The *interior* fixed point P at the intersection of the planes N_i , $i = 1, 2, 3$. Note that $AP = b$.

Again, we are interested only in those fixed points that lie in \mathbb{R}_+^3 . This includes each R_i , but not necessarily the Q_{ij} or P . Note that, apart from P and 0, each of the fixed points lies on the boundary $\partial\Sigma$ of Σ . Moreover, each coordinate plane is invariant under F , and the restriction of F to the i th coordinate plane $x_i = 0$ is a two-dimensional competitive Lotka-Volterra system, whose nullclines are precisely the intersections of the j th and k th nullclines of F with that coordinate plane (i, j, k distinct here). So $\partial\Sigma$ is composed of the one-dimensional carrying simplices of the restricted systems in each coordinate plane. See figure 5.

PROPOSITION 3.9. *The configuration of the planes N_i determines the dynamic behaviour of the flow at the fixed points R_i and Q_{ij} (whenever $Q_{ij} \in \mathbb{R}_+^3$).*

This is the three-dimensional version of proposition 3.1 of §3.1. The proof is analogous to that of proposition 3.1, relying on a geometric analysis of the partitioning of \mathbb{R}_+^3 by the planes N_i , and the relative positions of the fixed points.

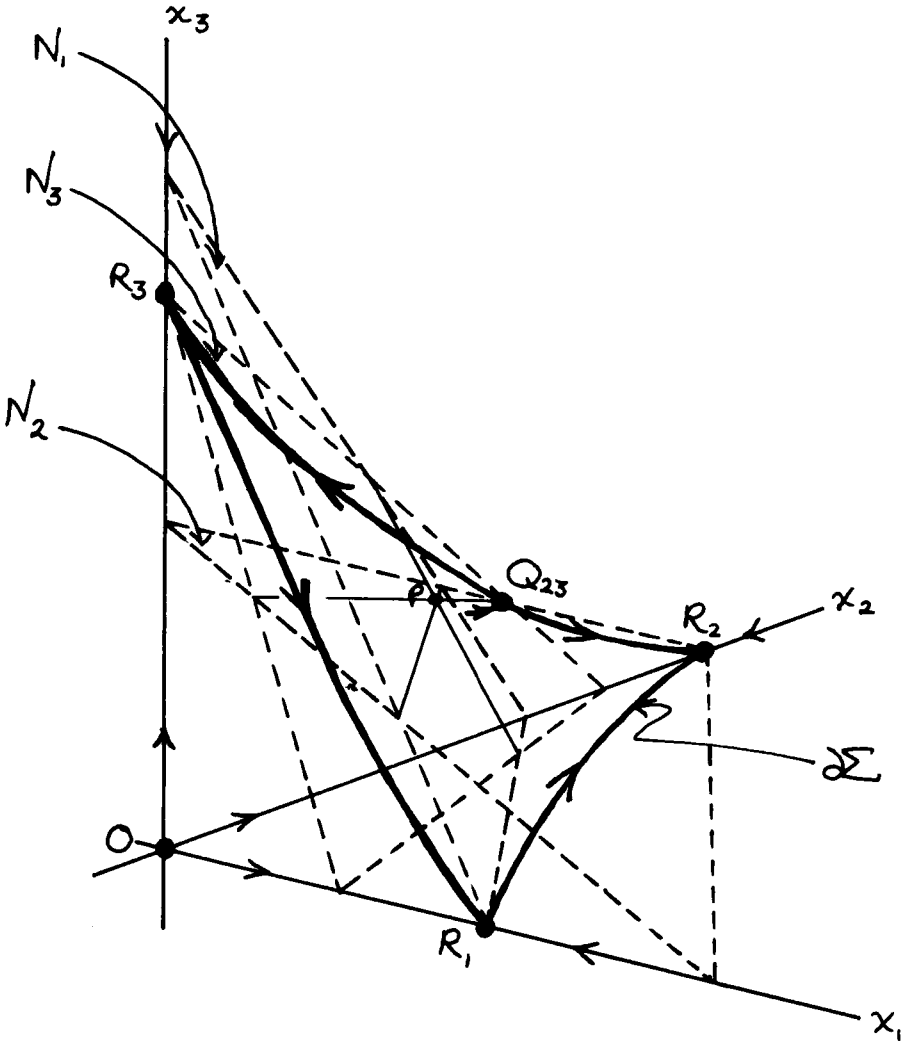


Figure 5: The behaviour at the fixed points on $\partial\Sigma$.

Proof. First consider the axial fixed point R_1 . The x_1 coordinate axis is an eigenspace of DF_{R_1} , along which R_1 attracts with associated eigenvalue $-b_1$. The invariance of the coordinate planes guarantees that the other two eigenvectors of DF_{R_1} lie one in each of the coordinate planes $x_2 = 0$ and $x_3 = 0$. Just as in the two-dimensional case, we determine whether R_1 attracts or repels along these eigendirections by considering where R_1 sits in the partition of \mathbb{R}_+^3 by each plane N_i ($i \neq 1$). For example, if R_1 lies in the bounded component of $\mathbb{R}_+^3 \setminus N_2$, then $\dot{x}_2 \geq 0$ in a neighbourhood of R_1 in \mathbb{R}_+^3 , and in particular, R_1 repels along the eigendirection in the $x_3 = 0$ coordinate plane. If, on the other hand, R_1 lies in the unbounded component of $\mathbb{R}_+^3 \setminus N_2$, then R_1 attracts along that eigendirection. In a similar fashion, we can determine all the behaviour at each R_i .

Now consider a planar fixed point $Q_{ij} \in \mathbb{R}_+^3$. Let's say Q_{23} . Again, the invariance of the coordinate plane $x_1 = 0$ guarantees two eigenvectors of $DF_{Q_{23}}$ in that plane. Indeed, the behaviour of the restricted system in the coordinate plane is determined by the behaviour at the axial fixed points R_2 and R_3 , as shown in the previous section. The behaviour along the third eigendirection of $DF_{Q_{23}}$, (which is *not* in the plane $x_1 = 0$), is determined in the usual way, by seeing whether Q_{23} sits in the bounded or unbounded component of $\mathbb{R}_+^3 \setminus N_1$. See figure 5. \square

As in §3.1 the proof of the proposition has given a geometric characterisation of the nullcline configuration, which easily translates into an algebraic characterisation as follows. Firstly, the position of the fixed point R_i relative to the plane N_j is given, as in §3.1, by

$$\operatorname{sgn}\left(\frac{b_i}{a_{ii}} - \frac{b_j}{a_{ji}}\right) = \operatorname{sgn}((AR_i)_j - b_j), \quad i \neq j$$

where $(AR_i)_j$ is the j th component of AR_i . Secondly, generalising this, note that if the fixed point Q_{ij} lay *on* the plane N_k we would have $(AQ_{ij})_k = b_k$, so the position of Q_{ij} relative to the plane N_k is given by

$$\operatorname{sgn}((AQ_{ij})_k - b_k), \quad i, j, k \text{ distinct}$$

where $(AQ_{ij})_k$ is the k th component of AQ_{ij} , as usual.

We can now define the nullcline configuration in terms of these values, ensuring again that it is independent of the labelling of the coordinate axes.

Note that this geometric nullcline analysis, together with its algebraic characterisation of the nullcline configuration, generalises in a straightforward manner to arbitrary dimension.

DEFINITION 3.10. Let $F \in CLV(3)$. The nullcline configuration of F is given by the values of $\operatorname{sgn}((AR_i)_j - b_j)$ and $\operatorname{sgn}((AQ_{ij})_k - b_k)$, for distinct i, j, k ; modulo permutation of the indices.

DEFINITION 3.11. Let $F, G \in CLV(3)$. We say that F and G are nullcline equivalent if and only if they have the same nullcline configurations.

This definition is clearly analogous to definition 3.4 of §3.1. Just as before, we call the equivalence classes under this relation the *nullcline classes*; we say that F is *nullcline stable* if and only if F has a neighbourhood of equivalents, and we call the open nullcline classes the *stable nullcline classes*.

PROPOSITION 3.12. Let $F \in CLV(3)$. Then F is nullcline stable if and only if $\text{sgn}((AR_i)_j - b_j)$, $\text{sgn}((AQ_{ij})_k - b_k) \neq 0$.

COROLLARY 3.13. The stable nullcline classes have open dense union in $CLV(3)$.

COROLLARY 3.14. There are 33 stable nullcline classes in $CLV(3)$.

Proposition 3.12 and corollary 3.13 are immediate. Corollary 3.14 is not so obvious. It is proved by counting all the combinatorial possibilities for the non-zero values of $\text{sgn}((AR_i)_j - b_j)$ and $\text{sgn}((AQ_{ij})_k - b_k)$, modulo permutation of the indices. This requires care, as these values are not independent.

It is interesting to note that this classification of $CLV(3)$ by nullcline equivalence is isomorphic to the topological classification of *all* two-dimensional Lotka-Volterra systems (see E. C. Zeeman [35]). However, as we shall see in §4, the added richness of structure afforded to us by the hyperbolic periodic orbits is in sharp contrast to the two dimensional situation where all periodic orbits are degenerate.

PROPOSITION 3.15. If $F \in CLV(3)$ is nullcline stable and has an interior fixed point P , then P is a simple fixed point.

The dynamical significance of this is that any limit set in $Int\Sigma$ is either P or a periodic orbit.

Proof. P is simple if and only if DF_P has no zero eigenvalues, that is $\det(DF_P) \neq 0$. Now F is given by

$$F_i(x) = x_i(b_i - (Ax)_i)$$

so $DF_P = -P^D A$ (since $AP = b$), where $P^D = (p_{ij})$ is the diagonal matrix with $p_{ii} = P_i$.

Assume (for contradiction) that $\det(DF_P) = 0$. Then $\det A = 0$ so that there is a linear dependence between the rows of A , and the planes N_i , which meet at P , have at least a line in common. But this means that F has a line of fixed points, contradicting nullcline stability. \square

We now use proposition 3.9 to describe - as far as possible - the dynamic behaviour of systems from each of the stable nullcline classes.

Let $F \in CLV(3)$ be nullcline stable. Recall that F has a two-dimensional invariant carrying simplex Σ , homeomorphic by radial projection to the unit simplex in \mathbb{R}_+^3 , and

globally attracting on $\mathbb{R}_+^3 \setminus \{0\}$. The non-zero fixed points of F all lie on Σ . Indeed, there is at most one fixed point P in $\text{Int}\Sigma$, the rest of them lie on the boundary $\partial\Sigma \subset \partial\mathbb{R}_+^3$ of Σ . To describe the dynamic behaviour of F , it is therefore enough to describe the behaviour of F restricted to Σ .

By proposition 3.9, the nullcline configuration determines the behaviour at each axial fixed point R_i , and this in turn determines the behaviour on $\partial\Sigma$. Moreover, if there are any planar fixed points $Q_{ij} \in \partial\Sigma$, then by proposition 3.9 again the nullcline configuration determines the dynamic behaviour on a neighbourhood of Q_{ij} in Σ .

Depending on the particular stable nullcline class in question, this may be enough information to fully describe the dynamics of F . For example, if F has no fixed point in $\text{Int}\Sigma$, then (by an application of Poincaré-Bendixson theory to Σ) F has no periodic orbits, and the behaviour on Σ is determined by that at the fixed points on $\partial\Sigma$. I.e. by the nullcline configuration.

On the other hand, if F has, say, an attracting fixed point $P \in \text{Int}\Sigma$, the question of periodic orbits of F remains open. We address this question in §4.

Figures 6 - 8 list representatives from each of the stable nullcline classes by the phase portraits - as far as they are yet determined - on Σ . More precisely, these are viewed as flows on the unit simplex in \mathbb{R}_+^3 , topologically equivalent via radial projection. A fixed point is represented by a closed dot \bullet if it attracts on Σ ; by an open dot \circ if it repels on Σ , and by the intersection of its hyperbolic manifolds if it is a saddle on Σ . The symbol \odot in figure 8 represents an area of unknown dynamics. That is: it represents the interior fixed point P , which may be attracting, neutral or repelling on Σ (see proposition 4.2), and a neighbourhood of P in which there may be any number of concentric periodic orbits.

PROPOSITION 3.16. *There are no periodic orbits in stable nullcline classes 1-25.*

Proof. The nullcline configurations 1-18 depicted in figure 6 are those in which the planes N_i do not meet in \mathbb{R}_+^3 , so that there is no interior fixed point. Thus we can apply Poincaré-Bendixson theory to the flow on Σ to conclude that there are no periodic orbits.

Now let $\dot{x} = F(x)$ be any system from classes 19-25, (depicted in figure 7) and consider its restriction to Σ . There is an interior fixed point P , together with two attracting and two repelling fixed points on $\partial\Sigma$. At each repellor, there must be a trajectory separating the basins of attraction of the two attractors. The omega limit set of this trajectory is either P , or a periodic orbit γ , attracting from one side. Similarly, at each attractor there is a trajectory separating the basins of repulsion of the repellers, whose alpha limit set cannot be γ . Thus there are no periodic orbits, and P is a saddle. \square

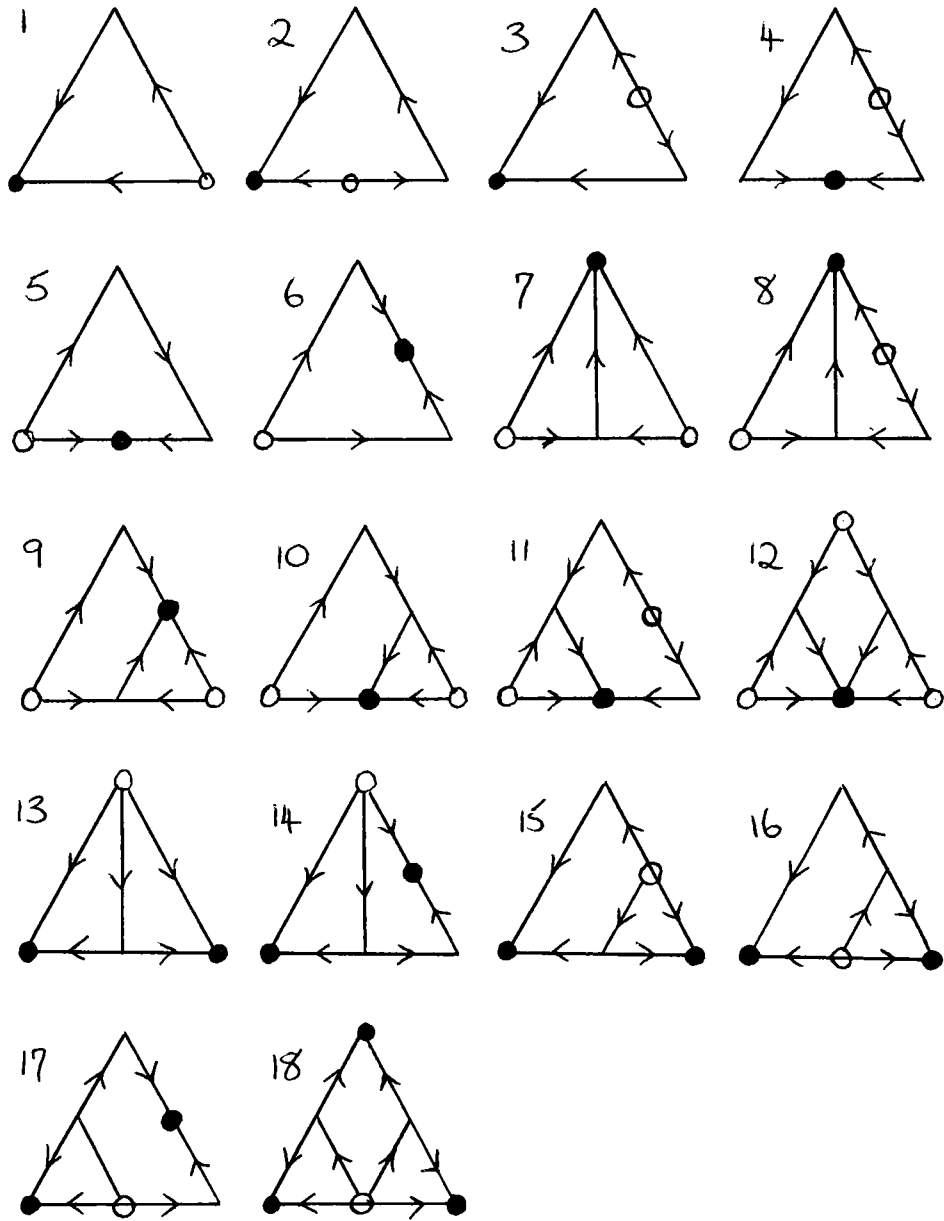


Figure 6: The phase portraits on Σ of the three-dimensional stable nullcline classes without interior fixed point. A fixed point is represented by a closed dot • if it attracts on Σ ; by an open dot ◦ if it repels on Σ , and by the intersection of its hyperbolic manifolds if it is a saddle on Σ .

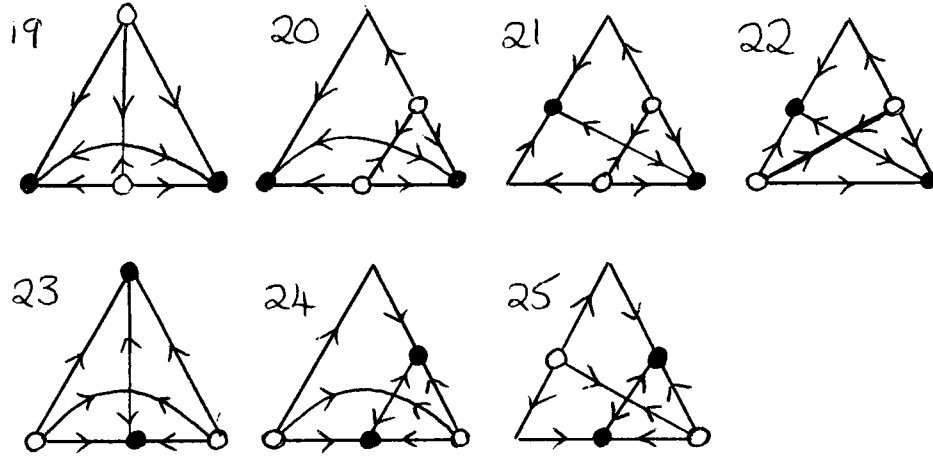


Figure 7: The phase portraits on Σ of the three-dimensional stable nullcline classes with interior saddle point. A fixed point is represented by a closed dot \bullet if it attracts on Σ ; by an open dot \circ if it repels on Σ , and by the intersection of its hyperbolic manifolds if it is a saddle on Σ .

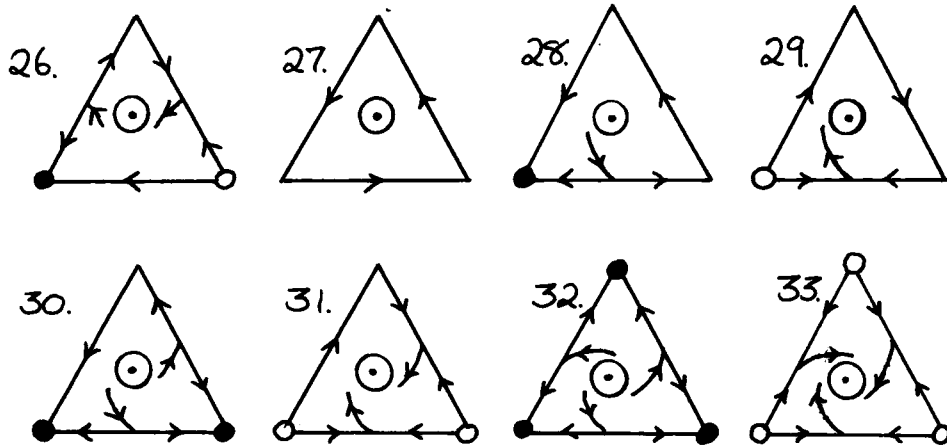


Figure 8: The phase portraits on Σ of the three-dimensional stable nullcline classes with interior fixed point of undetermined type. Fixed point notation as in figure 7, whilst the symbol \odot represents a region of unknown dynamics.

Conjecture 3.17. The stable nullcline classes 1-25 are stable topological classes.

In §4.3, we shall see in contrast that the stable nullcline classes 26-33 are refined by the stable topological classes according to periodic orbits.

Remark. The ecological significance of proposition 3.16 is that systems from nullcline classes 1-25 model three species interactions leading to the eventual extinction of one or even two of the species. There can be no stable coexistence, even of an oscillatory nature, of all three species.

4. Hopf Bifurcations in $CLV(3)$.

4.1 Algebraic Observations. In this section, we are concerned with the nullcline classes 26-33, and the question of whether or not they have periodic orbits.

In the last section, we extracted dynamic information from those geometric properties of the nullclines that are captured by the nullcline class. In order to exploit the finer geometry of the nullclines, we subdivide classes 26-33 into families of systems corresponding to fixed nullclines. Proposition 4.4 of this section states that generically, such a family contains a system with *no* periodic orbits (propositions 4.1 and 4.2 pave the way by simplifying the algebra), showing that the occurrence of periodic orbits in a given system cannot be predicted by the nullclines of that system alone. However, we shall show in §§4.2 and 4.3 that the nullclines *can* be used to predict the occurrence of Hopf bifurcations, and hence periodic orbits, in the family of systems corresponding to those fixed nullclines.

PROPOSITION 4.1. *For a system from any of the nullcline classes 26-33, we may assume that the interior fixed point P is at $(1,1,1)$.*

Proof. F is given by

$$F_i(x) = x_i(b_i - (Ax)_i) = x_i(A(P - x))_i, \quad \text{since } AP = b.$$

Make the linear change of coordinates $x \mapsto P^D x$, where $P^D = (p_{ij})$ is the diagonal matrix with $p_{ii} = P_i$. We shall ambiguously use 1 to denote the vector $(1,1,1)$ and the real number 1.

$$\begin{aligned} ((P^D)^{-1}FP^D)_i(x) &= \frac{1}{P_i}(P_i x_i(A(P^D 1 - P^D x))_i) \\ &= x_i(\tilde{A}(1 - x))_i, \quad \text{where } \tilde{A} = AP^D \\ &= \tilde{F}_i(x), \quad \text{say.} \end{aligned}$$

Thus we have a topological equivalence between F and a new competitive Lotka-Volterra system \tilde{F} with fixed point at $(1,1,1)$. It is clear (because P^D is diagonal) that F and \tilde{F} are also nullcline equivalent. \square

Thus we have reduced our parameter space from 12 to 9 dimensions. We exploit this by dispensing with the parameters b_i , and writing

$$F_i(x) = x_i(A(1-x))_i$$

Under this simplification F is completely determined by A , and we have $DF_P = (-P_j a_{ij}) = -A$. Henceforth, we shall abuse notation by using F and A interchangeably, as befits the context.

PROPOSITION 4.2. *For a system from any of the nullcline classes 26-33, $\det(DF_P) < 0$*

Proof. $\det(DF_P)$ is given by the product of the eigenvalues of DF_P , which we shall show is negative. Recall that $DF_P = -A$ and hence has strictly negative entries. By the Perron-Frobenius theorem, DF_P has a strictly negative simple eigenvalue λ , whose associated eigenvector is strictly positive. Now, Σ is invariant and is transverse to all strictly positive vectors, so the other two eigenvalues of DF_P are reflected by the behaviour of the flow on Σ . We consider the flow restricted to Σ , and show below that P is not a saddle. If, instead, P attracts, then both eigenvalues have negative real part. If P repels, they both have positive real parts. If P is neutral, they form a purely imaginary complex conjugate pair. In any case, the product $\det(DF_P|_{T_P\Sigma})$ of the two eigenvalues is positive and consequently $\det(DF_P) = \lambda \det(DF_P|_{T_P\Sigma}) < 0$.

Assume now that P is a saddle for the restricted flow on Σ . Since there are no other fixed points in $\text{Int}\Sigma$, we know by Poincaré-Bendixson theory that P has no homoclinic orbits, and there are no periodic orbits. Thus the omega limit set of the unstable manifold of P and the alpha limit set of the stable manifold of P both lie on $\partial\Sigma$. But in classes 27-33, we have an immediate contradiction, since the nullcline configuration ensures that $\partial\Sigma$ is either uniformly attracting, uniformly repelling, or has a neighbourhood in Σ foliated by periodic orbits. In class 26, the omega limit set of the unstable manifold could consist either of the attracting fixed point alone, or of the union of that fixed point with a saddle on $\partial\Sigma$. (The unique saddle with stable manifold in $\text{Int}\Sigma$). In either case, one trajectory of the stable manifold of P is then trapped inside an invariant region, the boundary of which is uniformly attracting. By repeating the previous argument, we reach a contradiction. \square

Remark. Recall that a system from nullcline classes 1-18 has no interior fixed point; whilst a system from classes 19-25 always has a saddle (on Σ) at P . This accounts for one positive and one negative eigenvalue of DF_P , and the Perron-Frobenius theorem implies that the third eigenvalue is negative; therefore $\det(DF_P) > 0$. Thus propositions 4.1 and 4.2 together tell us that to study the dynamic behaviour in classes 26-33, it is enough to consider those systems that can be written

$$\dot{x}_i = F_i(x) = x_i(A(1-x))_i, \text{ where } \det A = -\det(DF_P) > 0.$$

So we shall henceforth assume that F is of this form. With this notation, it is easy to see that the systems with exactly the same nullclines as $\dot{x} = F(x)$ are those of the form

$$\dot{x}_i = x_i(TA(1-x))_i$$

where $T = (t_{ij})$ is a diagonal matrix with strictly positive diagonal entries.

We can now define families of systems corresponding to fixed nullclines.

DEFINITION 4.3. If $\dot{x}_i = F_i(x) = x_i(A(1-x))_i$, and $T = (t_{ij})$ is a 3×3 diagonal matrix, define F^T by $F_i^T(x) = x_i(TA(1-x))_i$. Define the family $\mathcal{F}(F)$ through F by $\mathcal{F}(F) = \{F^T : t_{ii} > 0, i = 1, 2, 3\}$.

$\mathcal{F}(F)$ forms, in fact, a three-parameter family of systems, but by varying the diagonal entries of T one by one we can study it as a one-parameter family.

PROPOSITION 4.4. *For every F , there is a positive diagonal matrix T such that $F^T|_\Sigma$ is topologically equivalent to a two dimensional Lotka-Volterra system.*

Proof. Choose $t_{ii} = (\sum_{j=1}^3 a_{ij})^{-1}$, then TA is a matrix with all row-sums equal to 1. We show that if A has row-sums equal to 1, then $F|_\Sigma$ projects to a two dimensional Lotka-Volterra system.

Parametrise Σ by x_1 and x_2 , and consider the radial projection of $F|_\Sigma$ into the plane $x_3 = 1$, given (for $x_3 > 0$) by $x_i \mapsto y_i = \frac{x_i}{x_3}$, $i = 1, 2$. Recall from §2.1 that this projection is a homeomorphism, so that on Σ we can write $x_3 = x_3(x_1, x_2) = x_3(y_1, y_2)$. Thus we have:

$$\begin{aligned} \dot{y}_i &= \frac{d}{dt} \left(\frac{x_i}{x_3} \right) \\ &= \frac{1}{x_3^2} (x_3 \dot{x}_i - \dot{x}_3 x_i) \\ &= y_i ((A(1-x))_i - (A(1-x))_3) \\ &= y_i (1 - (Ax)_i - 1 + (Ax)_3), \text{ since } (A1)_i \text{ is the } i\text{th row sum of } A, \text{ and equals } 1. \\ &= x_3(y_1, y_2) y_i (\tilde{b}_i - (\tilde{A}y)_i), \text{ bringing out } x_3, \text{ and regrouping the terms to define} \\ &\quad \tilde{b}_i \text{ and the } 2 \times 2 \text{ matrix } \tilde{A}. \end{aligned}$$

Identifying the plane $x_3 = 1$ with \mathbb{R}^2 , this system is clearly topologically equivalent to the two dimensional Lotka-Volterra system $\dot{y}_i = y_i(\tilde{b}_i - (\tilde{A}y)_i)$ via the identity homeomorphism. Note that these new coefficients $\tilde{a}_{ij}, \tilde{b}_i$ are not necessarily positive, so the two-dimensional system is not necessarily competitive. \square

COROLLARY 4.5. For generic F , there is a system in $CLV(3)$ having the same nullclines as F , without periodic orbits.

The corollary follows from the familiar two-dimensional result (mentioned in the introduction), that the generic two-dimensional Lotka-Volterra system has no periodic orbits. In figure 9, we list representatives from stable nullcline classes 26-33 again, but this time using proposition 4.4 to choose representatives with *no* periodic orbits, in which case we can fill in the regions of previously unknown dynamics. In classes 26 and 27 there are two possible phase portraits. In the others the dynamics are fully determined.

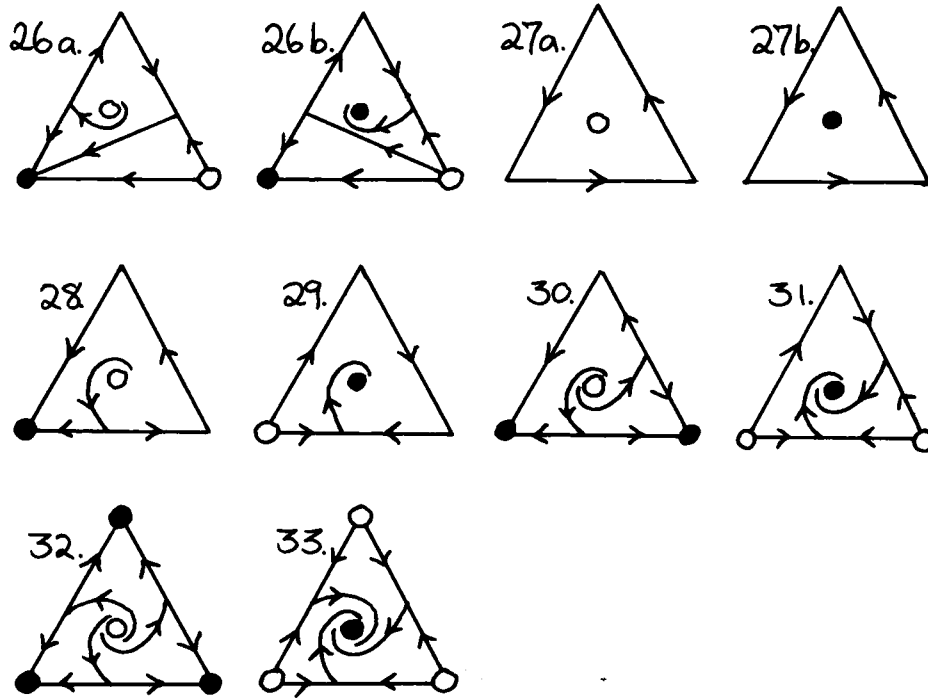


Figure 9: The phase portraits on Σ of representatives without periodic orbits from the three-dimensional stable nullcline classes 26-33.

The results of §4.3 show, in contrast, that there are also systems in $CLV(3)$ with periodic orbits. This means that we cannot tell whether a system has periodic orbits from its nullclines alone.

4.2 Families Without Hopf Bifurcations. In the preceding section, we defined families of systems within nullcline classes 26-33 corresponding to fixed nullclines. The results of this and the next section establish means of predicting from those nullclines whether a given family admits a Hopf bifurcation, and consequently, periodic orbits. In particular, we show that Hopf bifurcations occur in each of stable nullcline classes 26-31 (see §4.3), but *not* in stable nullcline class 32 (this section).

The prediction depends on the signs of the determinants of the principal two by two minors of any matrix A in the family. (Recall from proposition 4.1 that dynamically, F is completely determined by A , and for convenience we use F and A interchangeably). It is easy to see that these signs are independent of the choice of representative matrix A , and, in fact, can be determined from the nullcline positions as follows: The principal minor, A_{jk} , defined by

$$A_{jk} = \begin{pmatrix} a_{jj} & a_{jk} \\ a_{kj} & a_{kk} \end{pmatrix}, \quad j \neq k$$

represents the behaviour of the system restricted to the j - k th coordinate plane, where the two-dimensional analysis (§3.1) reveals that the determinant of the minor reflects the relative slopes of the j th and k th nullclines in this plane. In particular, recall that if these nullclines intersect at Q_{jk} on $\partial\Sigma$, then $\det(A_{jk}) > 0$ if and only if Q_{jk} attracts on the plane, and hence on $\partial\Sigma$; whilst $\det(A_{jk}) < 0$ if and only if Q_{jk} is a saddle on the plane, and hence repels on $\partial\Sigma$. We shall make repeated use of this relationship in the proofs that follow.

The main result of this section generalises easily to arbitrary dimension n . We state and prove it in this generalised form, for which we shall need the following notation. Let A be a non-singular $n \times n$ matrix with strictly positive entries. An n -dimensional competitive Lotka-Volterra system $F_i(x) = x_i(A(1-x))_i$, $i = 1, \dots, n$ on the closed non-negative cone \mathbb{R}_+^n will have an $(n-1)$ -dimensional carrying simplex Σ , homeomorphic via radial projection to the unit simplex in \mathbb{R}_+^n . The carrying simplex will have an $(m-1)$ -dimensional face in each m -dimensional coordinate plane, and the system restricted to that plane will be an m -dimensional competitive Lotka-Volterra system represented by an $m \times m$ principal minor of A . There will be an axial fixed point R_i at each vertex of Σ , at most one fixed point in the interior of each face, and one at $P = (1, \dots, 1)$. The $n \times n$ matrix A has strictly positive entries, and we denote by A_{jk} the principal 2×2 minor defined as above.

THEOREM 4.6. *Let $\dot{x}_i = F_i(x) = x_i(A(1-x))_i$, $i = 1, \dots, n$, with $\det A > 0$. If $\det(A_{jk}) < 0$ whenever $j \neq k$, then P has an unstable manifold of dimension at least 2.*

We prove theorem 4.6 using the following result about matrices.

PROPOSITION 4.7. *If $A = [a_{ij}]$ is an $n \times n$ matrix with $\det(A_{ij}) < 0$ for each principal 2×2 minor A_{ij} ($i \neq j$) of A , then A has an eigenvalue with negative real part.*

Proof. We prove this by contradiction. Assume that all the eigenvalues of A have non-negative real part. The characteristic polynomial of A is given by

$$\det(A - zI) = (-1)^n z^n + (-1)^{n-1} c_{n-1} z^{n-1} - \dots - c_1 z + c_0$$

where the coefficients c_i can be written either in terms of the entries a_{ij} of A , or in terms of the eigenvalues $\lambda_1, \dots, \lambda_n$ of A . In particular,

$$c_{n-2} = \sum_{i < j, j=2}^n \det(A_{ij}) < 0$$

by hypothesis (see Cullis [5, p. 307]), and

$$c_{n-2} = \sum_{i < j, j=2}^n \lambda_i \lambda_j \geq 0$$

by assumption. But these contradict! \square

Proof of theorem 4.6. The dynamic behaviour at $P = (1, \dots, 1)$ is given by the eigenvalues of $DF_P = -A$. By proposition 4.7, A has an eigenvalue with negative real part. But we have the added hypothesis that $\det A > 0$, so that A must have two eigenvalues with negative real part. Therefore $-A$ has two eigenvalues with positive real part, corresponding to an unstable manifold of P . \square

COROLLARY 4.8. *If each of the axial fixed points R_i is an attractor for F , then F has no other attracting fixed points.*

Proof. By first restricting our attention to the two dimensional coordinate planes, we see that the attraction of the R_i forces there to be a fixed point Q_{jk} on each of the one dimensional faces of Σ , and that Q_{jk} repels in that face. From the two-dimensional theory, we know that this means $\det(A_{jk}) < 0$ for each $j \neq k$. Now apply theorem 4.6 to each m -dimensional face of Σ , to see that F has no more attracting fixed points. \square

Reducing to three dimensions, we have:

COROLLARY 4.9. *Let $x_i = F_i(x) = x_i(A(1-x))_i$, $i = 1, 2, 3$, with $\det A > 0$. If $\det(A_{jk}) < 0$ whenever $j \neq k$, then P repels on Σ .*

Proof. For $F \in CLV(3)$, we know that Σ is a two-dimensional globally attracting invariant surface, and hence contains the unstable manifold of P . By theorem 4.6 this unstable manifold has dimension at least 2, and therefore must coincide (locally) with Σ . Thus P repels on Σ . \square

COROLLARY 4.10. *Within nullcline class 32, there are no Hopf bifurcations.*

Proof. Recall that every system in nullcline class 32 has three planar fixed points, each repelling on $\partial\Sigma$. Thus corollary 4.10 follows directly from corollary 4.9 in the light of the comment that Q_{jk} repels on $\partial\Sigma$ if and only if $\det(A_{jk}) < 0$. \square

This means that in nullcline class 32, periodic orbits are not produced at the interior fixed point, nor at $\partial\Sigma$ (the saddles prevent that), so that any periodic orbit that does occur must be the result of some peculiar “blue sky” bifurcation. Moreover, hyperbolic periodic orbits must occur in even numbers. This leads me to make the following conjecture, which I hope to prove by Liapunov type methods.

Conjecture 4.11. Systems in nullcline class 32 have no periodic orbits.

Remark. The ecological interpretation of corollary 4.8 is that if each of the n competing species, at carrying capacity, can resist invasion by small numbers of the others, then there can be no stable coexistence of more than one species, so that any coexistence must be oscillatory in nature. The conjecture, if true, would have the stronger meaning that when three such species interact, one of them must *always* dominate, leading to the extinction of the other two.

Note that there are also families of systems in classes 27-31 satisfying the hypotheses of theorem 4.6, but none in classes 26 or 33.

4.3 Families With Hopf Bifurcations. The following theorem is specific to three dimensions. Recall that A_{jk} denotes the principal minor

$$A_{jk} = \begin{pmatrix} a_{jj} & a_{jk} \\ a_{kj} & a_{kk} \end{pmatrix}, \quad j \neq k$$

of A .

THEOREM. *Let $x_i = F_i(x) = x_i(A(1-x))_i$, $i = 1, 2, 3$, with $\det A > 0$. If $\det(A_{jk})$, $j \neq k$ are not all of the same sign, then the family of systems $\mathcal{F}(F)$ admits a Hopf bifurcation. Moreover, we can exhibit a particularly simple one-parameter subfamily of $\mathcal{F}(F)$ which admits a Hopf-bifurcation.*

Coste *et al* [4] have proved that such bifurcations are, generically, non-degenerate, and thus give rise to hyperbolic periodic orbits. We prove theorem 4.12 below.

COROLLARY 4.13. *Within stable nullcline class 26, the family of systems corresponding to every set of null-clines admits a Hopf bifurcation, and consequently, periodic orbits.*

Proof. The corollary is immediate since any system in class 26 has a planar fixed point repelling on $\partial\Sigma$, and another attracting on $\partial\Sigma$, and thus has principal minors with determinants of opposite signs. \square

Note again that there are also families of systems in classes 27-31 satisfying the hypotheses of theorem 4.12, but none, of course, in classes 32 or 33.

Following the pattern of these theorems, we might naturally hope for a third result saying that (with F as above), if $\det(A_{jk}) > 0$ whenever $j \neq k$, then the family $\mathcal{F}(F)$ admits no Hopf bifurcations, thereby ruling out Hopf bifurcations in nullcline class 33. However there is no such result. I have found examples of families in that class which *do* admit Hopf bifurcations, and others which don't.

Proof of theorem 4.12. This proof is more subtle. As above, the behaviour at P is given by the eigenvalues of $DF_P = -A$, or equivalently, by those of A . From our family $\mathcal{F}(F)$ we choose a particular one-parameter family $F(t)$, with corresponding matrices $A(t)$. We then study the locus of the eigenvalues of $A(t)$ as we vary the parameter t . We show that for t_0 sufficiently small, the eigenvalues of $A(t_0)$ all have positive real part; whilst for t_1 sufficiently large $A(t_1)$ has a pair of eigenvalues with negative real part (or *vice versa*). Consequently, these eigenvalues must cross the imaginary axis as we perturb from $F(t_0)$ to $F(t_1)$. We show this crossing occurs with non-zero speed, and hence there is a Hopf bifurcation.

For simplicity, we change our notation slightly, and for a 3×3 matrix A , we let A^{ij} denote the 2×2 minor that remains after removing the i th row and j th column of A . With this notation, our hypothesis becomes $\det(A^{ii})$, $i = 1, 2, 3$ are not all of the same sign. To fix our ideas, consider the case $\det(A^{11}) > 0$ and $\det(A^{22}), \det(A^{33}) < 0$. The other cases will follow similarly. Recall that $\mathcal{F}(F)$ is the family determined by the matrices $\{TA \mid T = (t_{ij})$ a diagonal matrix with positive diagonal entries. $\}$. We shall consider the one-parameter subfamily given by fixing $t_{22} = t_{33} = 1$, and allowing $t_{11} = t$ to vary through all positive reals. So $F(t)_i(x) = x_i(A(t)(1-x))_i$,

$$\text{where } T = \begin{pmatrix} t & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \text{ and } A(t) = TA = \begin{pmatrix} ta_{11} & ta_{12} & ta_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

LEMMA 4.14. *At $t = 0$, the eigenvalues of $A(t)$ are $\lambda_0, \mu_0, 0$; where λ_0, μ_0 are strictly positive reals.*

The proofs of lemmas 4.14 - 4.16 follow shortly.

The eigenvalues of a matrix depend continuously on its entries, and thus for positive t_0 sufficiently close to 0, $A(t_0)$ has at least two eigenvalues with positive real part. But $\det A > 0$ by hypothesis, and $\det A(t) = t \det A > 0$ for $t > 0$, so that the product of the eigenvalues of $A(t_0)$ is positive, and hence all three eigenvalues of $A(t_0)$ must have positive real part. Thus P is attracting for $F(t_0)$.

LEMMA 4.15. *As $t \rightarrow \infty$, the eigenvalues of $A(t)$ tend to λ_1, μ_1, ∞ ; where λ_1, μ_1 both have strictly negative real part.*

As before, the eigenvalues of $A(t)$ depend continuously on the entries of $A(t)$, and hence on t . So for sufficiently large t_1 , $A(t_1)$ has two eigenvalues with negative real part, and P is repelling on Σ for $F(t_1)$. Consequently, as t varies from t_0 to t_1 , two of the eigenvalues of $A(t)$ vary continuously from having positive real part to negative real part, and necessarily cross the imaginary axis on their way. Moreover, they do not cross the axis at zero, since $\det A(t) \neq 0$ for $t \neq 0$, and thus must cross as a non-zero complex conjugate pair.

LEMMA 4.16. *There is a unique parameter value at which the eigenvalues of the family $\{A(t)\}$ cross the imaginary axis. Moreover, this crossing occurs with non-zero speed.*

This corresponds to a Hopf bifurcation in the family of systems $\{F(t)\}$, and the theorem is proved. \square

Proof of lemma 4.14. $A(0)$ is the continuous limit of positive matrices $A(t)$, and thus has a non-negative eigenvalue, dominating the moduli of the other eigenvalues, which is the continuous limit of the Perron-Frobenius eigenvalue of the matrices $A(t)$. Now,

$$A(0) = \begin{pmatrix} 0 & 0 & 0 \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

and so the characteristic polynomial of $A(0)$ is given by $\det(A(0) - zI) = -z \det(A^{11} - zI)$. Therefore the eigenvalues of $A(0)$ are $\lambda_0, \mu_0, 0$; where λ_0, μ_0 are the eigenvalues of the 2×2 minor A^{11} , and one of λ_0, μ_0 must be the non-negative Perron-Frobenius eigenvalue mentioned above. By hypothesis, $\lambda_0 \mu_0 = \det(A^{11}) > 0$, and thus both of λ_0, μ_0 must be positive. \square

Proof of lemma 4.15. We first show that the Perron-Frobenius eigenvalue ν_t of $A(t)$ grows with t . There are many ways of seeing this, but the neatest uses Gerschgorin's theorem [3], which, although a beautiful and basic tool of numerical analysis, seems to be less well known in the world of pure mathematics. For this reason we state it here.

THEOREM 4.17 (GERSCHGORIN). *Given an $n \times n$ matrix $A = (a_{ij})$, define the i th Gerschgorin disc D_i in the complex plane to be the closed disc of radius $\sum_{j \neq i} |a_{ij}|$ centered at the point a_{ii} . Each Gerschgorin disc contains an eigenvalue of A , and moreover, for any distinct i_1, \dots, i_r , there are at least r eigenvalues of A in $\bigcup_{k=1}^r D_{i_k}$. (Eigenvalues are counted with multiplicity.)*

Note that we used the rows of A to define the Gerschgorin discs. By applying the theorem to the transpose of A , we see that we could equally well have defined them using the columns of A .

We now apply Gerschgorin's theorem to $A(t)$, concentrating in particular on the disc defined by the first column of $A(t)$. Recall that

$$A(t) = \begin{pmatrix} ta_{11} & ta_{12} & ta_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

so that $A(t)$ has an eigenvalue ν_t in the disc of radius $a_{21} + a_{31}$, centre ta_{11} . That is: $|ta_{11} - \nu_t| \leq a_{21} + a_{31}$. Thus ν_t grows with t , and as $t \rightarrow \infty$, $\nu_t \rightarrow \infty$.

Now consider the Gerschgorin discs D_2 and D_3 defined by the second and third rows of $A(t)$ respectively. These are independent of t , and whilst ν_t grows unboundedly, the other two eigenvalues λ_t, μ_t are trapped in the compact union $D_2 \cup D_3$.

Now, λ_t, μ_t are either a complex conjugate pair, in which case they correspond to an invariant plane; or they are distinct reals, in which case their eigenspaces span an invariant plane. In either case, we restrict our attention to that invariant plane, $N(t)$, to discover more about λ_t and μ_t . To determine the plane, note that $N(t)$ depends continuously on t , and consider the matrices $\frac{1}{t}A(t)$. For each t , $\frac{1}{t}A(t)$ clearly has the same invariant planes as $A(t)$, and as $t \rightarrow \infty$,

$$\frac{1}{t}A(t) \rightarrow B = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

B has eigenvalue 0 with corresponding eigenspace $N = \{x \mid (Bx)_1 = 0\}$, which we recall is parallel to the first nullcline N_1 of the systems $F(t)$. Thus the invariant planes $N(t)$ of $A(t)$ tend to N as $t \rightarrow \infty$.

Let $n(t) : R^2 \rightarrow N(t)$, and $n : R^2 \rightarrow N$ be the parametrisations by (x_2, x_3) of $N(t)$ and N respectively; and let $\pi : R^3 \rightarrow R^2$ be projection onto the (x_2, x_3) coordinate plane, so that $\pi \mid N(t) = (n(t))^{-1}$, for all t . Then $\pi \circ A(t) \circ n(t)$ is a linear vector field on $x_1 = 0$, topologically conjugate to the restriction $A(t) \mid N(t)$. But for sufficiently large t_1 , we can approximate $N(t_1)$ arbitrarily closely by N , and we can approximate the vector field $\pi \circ A(t_1) \circ n(t_1)$ accordingly by $\pi \circ A(t_1) \circ n$. Now

$$\begin{aligned} \pi \circ A(t_1) \circ n \begin{pmatrix} x_2 \\ x_3 \end{pmatrix} &= \begin{pmatrix} \frac{-a_{21}}{a_{11}}(a_{12}x_2 + a_{13}x_3) + a_{22}x_2 + a_{23}x_3 \\ \frac{-a_{31}}{a_{11}}(a_{12}x_2 + a_{13}x_3) + a_{32}x_2 + a_{33}x_3 \end{pmatrix} \\ &= \frac{1}{a_{11}} \begin{pmatrix} \det(A^{33}) & \det(A^{32}) \\ \det(A^{23}) & \det(A^{22}) \end{pmatrix} \begin{pmatrix} x_2 \\ x_3 \end{pmatrix} \end{aligned}$$

so that the sum of the eigenvalues of $\pi \circ A(t_1) \circ n$ is given by $\text{trace}(\pi \circ A(t_1) \circ n) = \frac{1}{a_{11}}(\det(A^{22}) + \det(A^{33})) < 0$, by hypothesis. Thus $\pi \circ A(t_1) \circ n$ has at least one eigenvalue with strictly negative real part bounded away from 0, and consequently so do $\pi \circ A(t_1) \circ n(t_1)$, $A(t_1) \mid N(t_1)$, and $A(t_1)$ itself. But $\det A(t_1) > 0$, so $A(t_1)$ must have two eigenvalues with strictly negative real part. \square

Proof of lemma 4.16. We know from lemmas 4.14 and 4.15 that the eigenvalues of the family $\{A(t)\}$ must cross the imaginary axis at least once. Let s be a parameter value at which such a crossing occurs. That is, for t in a sufficiently small neighbourhood U of s , $A(t)$ will have a complex conjugate pair of eigenvalues, and we denote by $\lambda(t)$ the eigenvalue with positive imaginary part. Then λ is a continuous complex valued function

on U such that for $t < s$, $\operatorname{Re}(\lambda(t)) > 0$; $\operatorname{Re}(\lambda(s)) = 0$; and for $t > s$, $\operatorname{Re}(\lambda(t)) < 0$. The crossing occurs with non-zero speed iff $\frac{d}{dt}(\operatorname{Re}(\lambda(t)))|_s \neq 0$.

We show below that the non-real eigenvalues of the family $\{A(t)\}$ lie on a quartic curve in the complex plane, disjoint from the imaginary axis except for transverse intersections at $\lambda(s)$ and $\overline{\lambda(s)}$. Thus s is unique, and $\frac{d}{dt}(\operatorname{Re}(\lambda(t)))|_s = 0$ iff $\frac{d}{dt}(\lambda(t))|_s = 0$, which leads to a contradiction.

The characteristic polynomial of $A(t)$ can be written

$$\det(A(t) - zI) = -zg_1(z) + tg_2(z)$$

where each $g_i : \mathbb{C} \rightarrow \mathbb{C}$ is a quadratic function, independent of t . With this notation, z is an eigenvalue of $A(t)$ iff

$$-zg_1(z) + tg_2(z) = 0 \Leftrightarrow t = \frac{zg_1(z)}{g_2(z)}$$

We use this to define a new (meromorphic) function G on \mathbb{C} by

$$G(z) = \frac{zg_1(z)}{g_2(z)}$$

so that the eigenvalues of $A(t)$ are given precisely by $G^{-1}(t)$. The locus of the eigenvalues of our family $\{A(t) : t > 0\}$ is given by $G^{-1}(\operatorname{Int}\mathbb{R}_+)$, and this lies inside $G^{-1}(\mathbb{R})$. But

$$\begin{aligned} G(z) \in \mathbb{R} &\Leftrightarrow G(z) = \overline{G(z)} \\ &\Leftrightarrow zg_1(z)g_2(\overline{z}) - \overline{z}g_1(\overline{z})g_2(z) = 0 \end{aligned}$$

Writing $z = x + iy$ ($x, y \in \mathbb{R}$) and regrouping terms, it is easy to show that

$$G(z) \in \mathbb{R} \Leftrightarrow yH(x, y) = 0$$

where $H : \mathbb{R}^2 \rightarrow \mathbb{R}$ is a quartic function, symmetric in y . Thus the locus of the eigenvalues of the family $\{A(t)\}$ lies on the union of the real axis with the quartic curve \mathcal{H} given by $H(x, y) = 0$. The fact that non-real eigenvalues occur in conjugate pairs is reflected by the symmetry of \mathcal{H} with respect to the real axis.

In particular, \mathcal{H} intersects the imaginary axis \mathcal{J} at $\lambda(s)$, and is parametrised in a neighbourhood of $\lambda(s)$ by $\lambda : U \rightarrow \mathbb{C}$. Assume (for contradiction) that this intersection is not transverse. Then \mathcal{H} crosses \mathcal{J} tangentially at $\lambda(s)$, so the intersection has multiplicity $m > 2$. By symmetry, there is another intersection of multiplicity m at $\overline{\lambda(s)}$, so the line \mathcal{J} intersects the quartic \mathcal{H} at least $2m$ times. But then Bézout's theorem [9] implies $2m \leq 4 \Rightarrow m \leq 2$. Contradiction! Thus \mathcal{H} is transverse to \mathcal{J} at $\lambda(s)$.

Now assume that \mathcal{H} intersects \mathcal{J} again. By lemmas 4.14 and 4.15, together with symmetry, this means that \mathcal{H} intersects \mathcal{J} at least 6 times, contradicting Bézout's theorem. Thus s is unique.

Finally, assume (for contradiction) that $\frac{d}{dt}(Re(\lambda(t)))|_s = 0$. By transversality at $\lambda(s)$ and $\overline{\lambda(s)}$, this implies that $\lambda'(s), \overline{\lambda'(s)} = 0$, where λ' denotes $\frac{d\lambda}{dt}$. Moreover, $\lambda(s) + \overline{\lambda(s)} = 0$ since $\lambda(s)$ is purely imaginary. Recall that we can write the coefficients of the characteristic polynomial of $A(t)$ in terms of either the eigenvalues or the entries of $A(t)$. For $t \in U$ this gives

$$\det(A^{11}) + t(\det(A^{22}) + \det(A^{33})) = \lambda(t)\overline{\lambda(t)} + \overline{\lambda(t)}\nu(t) + \nu(t)\lambda(t)$$

where $\nu(t)$ is the Perron-Frobenius eigenvalue of $A(t)$. Differentiating this expression at s , we have

$$\begin{aligned} \det(A^{22}) + \det(A^{33}) &= \lambda'(s)(\overline{\lambda(s)} + \nu(s)) + \overline{\lambda'(s)}(\lambda(s) + \nu(s)) + (\lambda(s) + \overline{\lambda(s)})\nu'(s) \\ &= 0 \text{ by assumption.} \end{aligned}$$

But $\det(A^{22}) + \det(A^{33}) < 0$ by hypothesis, and hence we have a contradiction. \square

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